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Development of a surplus production model to assist management of the walleye fishery in Lake Nipissing

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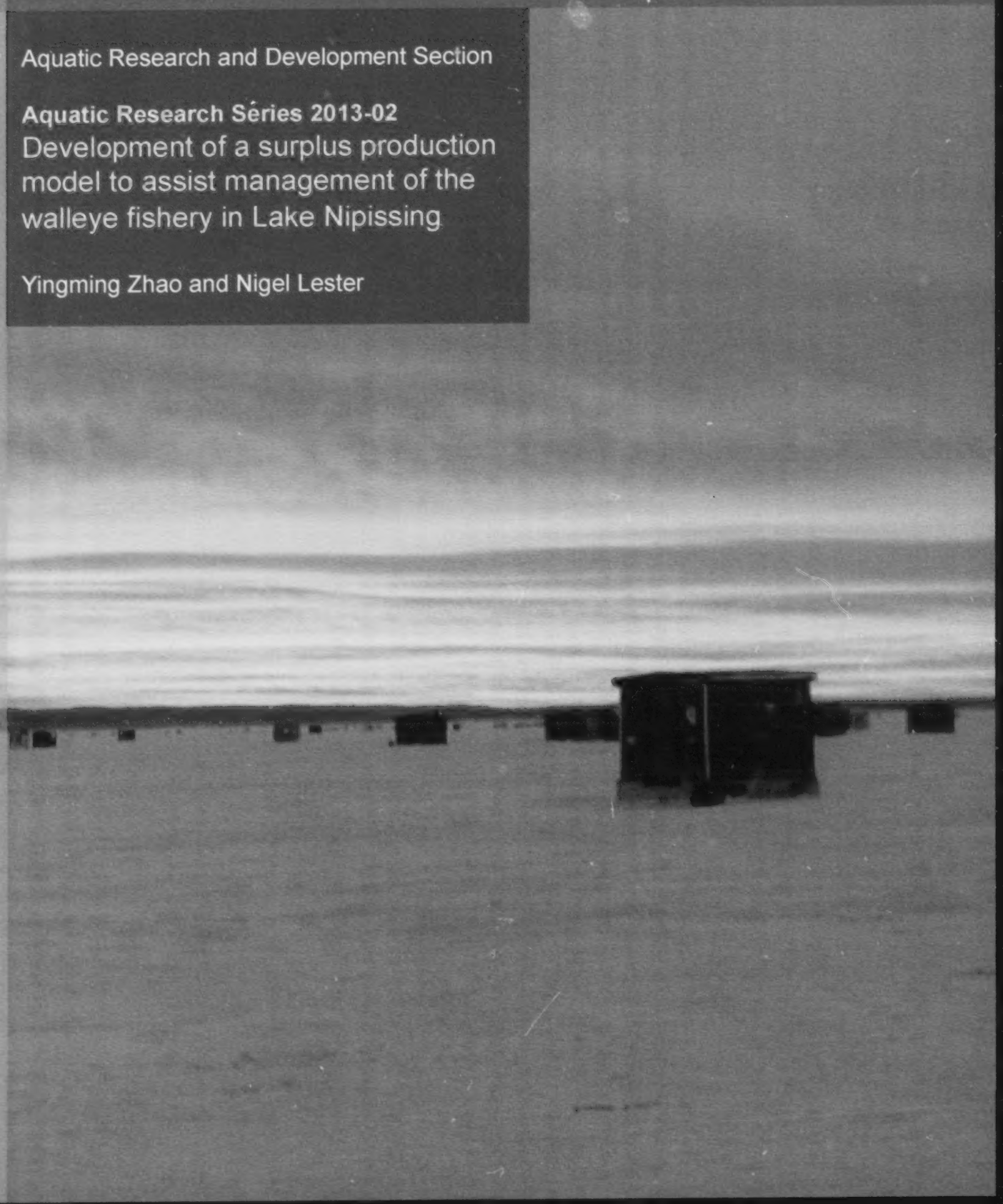

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Abstract

In this study, we developed a surplus-production model to assess the walleye stock in Lake Nipissing. Two indices of stock biomass were used in the model: (1) harvest per unit effort (HPUE, kg/hour) of recreational fishers from 1976 to 2011; and (2) Fall Walleye Index Netting catch per unit effort (CUEW, kg/net) from 1998 to 2011. We compared two model configurations (Graham-Schaefer logistic model and Pella-Tomlinson model with a specified shape parameter) and two forms of catchability (density-dependent and constant). The two model configurations with constant catchability (for both angling and index netting) fitted the observed data almost equally well. Both models showed that the population biomass has been declining since 1976. The current population biomass is estimated to be 18-20% of the biomass expected to produce the maximum sustainable yield (MSY). The estimated fishing mortality in 2011 is more than twice as high as the rate which maximizes harvest (F_{msy}). The results indicate that Lake Nipissing walleye population is over-exploited. Simulations based on model parameters predict that if the fishing rate is reduced to F_{msy}, it will take about 50 years to rebuild the population to the biomass that maximizes the sustainable yield.

Résumé

Dans cette étude, nous avons développé un modèle de production excédentaire pour évaluer le stock de doré jaune dans le lac Nipissing. Deux indices de la biomasse du stock ont été utilisés dans le modèle : (1) capture par unité d'effort (CPUE, kg/heure) de la pêche sportive de 1976 à 2011, et (2) décompte automnal de prises de doré au filet (DAPDF, kg/filet) de 1998 à 2011. Nous avons comparé les deux configurations du modèle (modèle logistique de Graham-Schaefer et modèle de Pella-Tomlinson avec un paramètre de forme déterminée) et deux sortes de capturabilité (dépendante de la densité et constante). Les deux configurations de modèles avec une capturabilité constante (pour la pêche sportive et le décompte de prises au filet) étaient pratiquement l'une aussi que l'autre compatibles avec les données observées. Les deux modèles montrent que la biomasse de la population baisse depuis 1976. La biomasse de la population actuelle est estimée à entre 18 et 20 % de la biomasse qui devrait produire le rendement équilibré maximal (MSY). La mortalité estimée par pêche en 2011 était plus du double du taux qui permet de maximiser la récolte (F_{msy}). Les résultats indiquent que la population de doré jaune dans le lac Nipissing est surexploitée. Les simulations fondées sur les paramètres des modèles montrent que si le taux de pêche était réduit à F_{msy}, il faudrait attendre une cinquantaine d'années avant que la population retrouve la biomasse nécessaire pour maximiser le rendement équilibré.

Background

Walleye (*Sander vitreus*) is a key species of the Lake Nipissing fish community and supports significant fisheries for both First Nations and recreational fisheries. The recreational fishery attracts a large number of tourists to the area each year. First Nations harvest the species for ceremonial, subsistence and commercial purposes. The commercial fisheries have become the livelihood for some Nipissing First Nation families.

Assessment and management of Lake Nipissing walleye resources were initiated as early as 1960 by Ontario Ministry of Natural Resources (OMNR), and focussed on the recreational fishery for the first forty years. Since the inception of the management programme for the walleye recreational fishery, the fishing regulations have been revised several times, affecting the opening and closing season dates, size limit restrictions, and daily catch and possession limits.

Nipissing First Nations commercial fishing on Lake Nipissing pre-dates European settlement. However, reliable quantitative data on this fishery only exists for the past decade. Nipissing First Nations started regulation of its commercial fishery in 2004 and the regulations applied to open seasons for the gillnet fishery. Since 2004, a comprehensive Fisheries Law with a full complement of regulations has been implemented. These regulations include an annual lake-wide harvest quota system, where quota is determined by assessing the changes in walleye abundance index derived from a fall gillnet index survey operated by the OMNR since 1998. The performance of previous year's quota achievement is also taken into consideration when setting the current year's quota.

A recent decline in walleye has been reported. In the Lake Nipissing Interim Fisheries Management Plan 2007-2010, resource managers considered the walleye population "in a stressed state". However, lack of a population model for the species prevented managers from better understanding of the population dynamics, assessing the stock status and evaluating different harvest policies. A recent review (Morgan, 2012) of all existing data from 1967 to 2011 documented that the walleye population has been in decline for many years. This study was designed to develop a population dynamic model for Lake Nipissing walleye. This type of modeling was suggested at several consultation meetings. After assessing the quantity, quality and limitations of available data from both fishery-dependent and independent surveys, we decided to develop a biomass-based (surplus production) population dynamic model. Our objectives were to:

(1) estimate intrinsic growth rate and carrying capacity and apply these parameters in deriving historical trends in population biomass and estimating maximum sustainable yield and optimal exploitation rate,
(2) simulate future population growth and impacts of fishing on the population growth using the surplus production model under different fishery management scenarios, and
(3) provide scientific recommendations about the future development of a more sophisticated stock assessment model, such as an age-structured model.

Methods

Surplus Production Model

The surplus production model is a biomass-based stock assessment model. The model combines three important processes i.e. recruitment, growth, and natural mortality into a single surplus production function (Quinn and Deriso, 1999). We applied two forms of surplus production model to Lake Nipissing walleye. The first is referred to as the Graham-Schaefer model. The second is the Pella-Tomlinson (PT) model. As described below, the PT model is a generalization of the Graham-Schaefer model.

The differential form of the first surplus model (i.e., Graham-Schaefer logistic model) is:

$$dB_t/dt = r*B_t*(1-B_t/K) - H_t \quad \text{and} \quad H_t = F_t*B_t = q*E_t*B_t \qquad (1a)$$

where B_t and H_t are mean biomass and total fishery harvest at year t, respectively; r is intrinsic growth rate; K is carrying capacity; F_t is fishing mortality; E_t is fishing effort at year t; and q is the catchability coefficient of fishing gear. Population intrinsic growth rate (r) is determined by combining the effect of pre-maturation survival, adult fecundity, and age (or size) at maturity (Myers and Mertz, 1998). Carrying capacity (K) is related to environmental conditions, such as habitat and food resources.

In the absence of fisheries harvest (i.e., H=0), there are three parameters in the model: intrinsic growth rate, carrying capacity, and biomass at the beginning of time series (B_0). In this case, population biomass will increase in a sigmoid pattern until it reaches its carrying capacity. Harvesting introduces another model parameter, fishing mortality, which equals the product of fishing effort and catchability. After incorporating fishing mortality, population biomass fluctuates year by year driven by the intensity of the harvest.

For convenience, maximum sustainable yield (MSY) can replace the intrinsic growth rate (r) through the relationship r = 4*MSY/K, and be estimated as a parameter in the model (Fletcher, 1978). Substituting for r in equation 1 gives

$$dB_t/d_t = 4*MSY/K*(B_t/K)*[1 - (B_t/K)] - H_t \qquad (1b)$$

This model, the Graham-Schaefer model, assumes a symmetric relationship (i.e. a parabolic function) between population surplus production and biomass. Consequently, maximum surplus production (i.e. MSY) occurs when biomass (BMSY) is half of carrying capacity (Figure 1a, b). This symmetric relationship exists because the Graham-Schaefer model assumes equilibrium biomass decreases linearly as fishing mortality increases (Figure 1b). Pella and Tomlinson (1969) proposed a more general model which relaxes this assumption. They introduced a shape parameter (n) such that

$$dB_t/d_t = \gamma*MSY*(B_t/K)*[1 - (B_t/K)^{n-1}] - H_t, \qquad (2)$$

where $\gamma = n^{n/(n-1)}/(n-1)$. When n = 2, the Pella and Tomlinson (PT) model reduces to a Graham-Schaefer model; when n < 2, MSY occurs at a biomass level less than half of carrying capacity (i.e. $B_{MSY} < 0.5*K$); and when n > 2, $B_{MSY} > 0.5*K$. In cases where n <> 2, biomass does not decrease linearly with equilibrium fishing mortality, being concave up or down depending on value of n (Figure 1a, b). However, the data available for a standard surplus production modelling procedure may not provide sufficient information to estimate the shape parameter (n), in which case it must be estimated from auxiliary information. Thorson et al. (2012) carried out a metadata analysis on 147 fish stocks and concluded that, for marine Perciforms, the shape parameter (n) was around 1.064. We used this value when fitting a Pella-Tomlinson model to Lake Nipissing walleye data.

A surplus production model is a fishery model of simplified population dynamics. It ignores the complexities of age structure and spatial structure and assumes compensatory population growth. One attractive feature of the model is that it can provide fishery managers with some important management parameters: the maximum sustainable yield, the biomass (B_{msy}) producing MSY, the level of fishing rate (F_{msy}) or effort (E_{msy}) that drives the population to the biomass level producing MSY, and the maximum exploitation rate (F_{ext}) that the population can sustain. In addition, it predicts the trajectory of population growth, the status of current population, and its surplus levels. However, its ability to accurately describe and predict the dynamics of fish populations depends greatly on the nature of the available data (see the following paragraph for details). This type of model is often used when catch-at-age information is not available to develop a more sophisticated age-structured model.

Compared to other fisheries models, surplus production models need relatively little data to estimate population parameters: only total harvest and an index of population biomass are required to estimate historical biomasses, r (or MSY), K, and q (given fishing effort data are available). Three approaches have been developed to estimate these parameters: (a) equilibrium assumption—abandoned because few fish populations are in equilibrium, (b) multiple linear regression, and (c) time-series fitting. Although the last two approaches don't assume that

the fish population is at equilibrium, their estimation accuracy depends greatly on data quality and the fishery perturbation history. Hilborn (1979) and Hilborn & Walters (1992) demonstrated that when the observed data lack sufficient contrast (i.e. different combinations of population size and fishing effort), the estimators may be highly correlated and not well defined. Monte Carlo simulations based on scenarios that represent four types of perturbation history provided a useful reference for identifying issues associated with surplus production modelling (Hilborn & Walters, 1992),

Scenario 1: One-way Trip: the observed effort increases, and the abundance index decreases. For this scenario, the q and r estimates can be well defined but K is often very poorly defined.

Scenario 2: Up and Down Isocline: the observed effort goes up and down and the corresponding abundance goes down and up. In this case, all three parameters (q, r, and K) cannot be well defined but their combination (e.g. MSY, effort at MSY) can be established.

Scenario 3: Recovery Only: population at very low abundance and very low effort levels. The r can be estimated but K and q are uncertain.

Scenario 4: Good Contrast: population experienced a broad range of abundance and effort levels. Estimates for all 3 parameters (r, K, and q) are well defined.

The parameters can be estimated by assuming measurement errors in catch or catch-per-unit-effort (CPUE) and/or process errors.

Data for the Development of a Surplus Production Model for the Lake Nipissing Walleye population

For the Lake Nipissing walleye population, a time period from 1976 to 2011 was selected for surplus production modelling. During this period, the recreational fishery from both winter and summer seasons provided relatively complete observations of annual harvest and fishing effort. Harvest-per-unit-effort (HPUE) from the recreational fishery was used as an index of the population biomass (B): HPUE = q B. The harvest from the Nipissing First Nation commercial gillnet fishery has been reported annually since 1995. Total annual harvest in this period was calculated by summing the harvests from the two fisheries (i.e. commercial and recreational). The data used for this study are presented in the Appendix. Annual fishing mortality was estimated by dividing annual harvest by the population biomass.

The Lake Nipissing Walleye population has been surveyed and assessed annually since 1998 using the OMNR provincial standard Fall Walleye Index Netting (FWIN) protocol. The FWIN method (Morgan, 2002) uses a standard gillnet with 8 mesh sizes, applies a stratified survey design, covers the entire lake, and starts annually when water surface temperature cools to 15°C in fall. The survey produces a fall abundance index (survey catch-per-unit-effort, CPUE) for walleye larger than 300mm total length, the typical size recruiting to the fisheries. To use both walleye indices (i.e. recreational HPUE from 1976 to 2011 and FWIN survey CPUE 1998 to 2011) for surplus production modelling, a weighting factor needs to be assigned. Because the overlap period is only 13 years (1998 to 2011), we separated the entire time series into two periods, 1976 to 1997 and 1998 to 2011. For the first period, only recreational HPUE exists and its weight was set high. For the second period, we applied three combinations of weighting factors which varied the influence of FWIN CPUE. An exploratory analysis showed that the model encountered numerical convergence problems when the weighting factor for FWIN CPUE was high. Therefore, we tested only two combinations of weighting factors: 5:5:5 and 5:5:1, where the three numbers are weights assigned to following three indices of abundance: recreational HPUE for 1976-1997, recreational HPUE for 1998-2011, and survey CPUE for 1998-2011. Thus, the second combination indicates a lower weighting of the FWIN CPUE, relative to recreational HPUE. A Gaussian error structure was assumed for the both HPUE and CPUE in the maximum likelihood estimation procedure such that

$$HPUE = q_1 * B + \varepsilon_1 \quad (3)$$
$$CPUE = q_2 * B + \varepsilon_2 \quad (4)$$

where q_1 and q_2 are catchability coefficients for recreational fishing and survey gillnetting, respectively, and ε_1 and ε_2 are their associated normal random errors. For recreational fishing, we assumed catchability might be inversely density-dependent (i.e. catchability increases as biomass decreases). We tested for three levels of density dependence by setting:

(1) $q_1 = c$: constant with no density-dependence,
(2) $q_1 = c*B^{-0.5}$: strong density-dependence, and
(3) $q_1 = c*B^{-0.36}$: weak density-dependence.

The resulting six model configurations (2 levels of abundance index weighting times 3 models of angling catchability) were run for each of two surplus production models (Graham-Schaefer and Pell-Tomlinson), giving a total of twelve model configurations (Table 1). The Akaiki Information Criterion corrected for sample size (AICc) was adopted to select among the model configurations (Burnham and Anderson, 2002):

$$AICc = -2*\log(Likelihood)+2*k*n/(n-k-1),$$

where k is number of parameters and n is sample size

Fishery Management Simulation

We used the estimated model parameters and the population biomass estimates for the most recent year (2012) to predict future walleye abundance under different harvesting scenarios. This exercise contrasted two harvest strategies: (1) constant harvest rate and (2) constant absolute harvest. Given a constant harvest rate, the harvest-biomass line and surplus production-biomass curve can have at most one intersection point (A in Figure 2a) which is a stable equilibrium. The population will approach this equilibrium biomass through time. For this scenario, we assumed a range of harvest rates (e.g., 0, $0.5*F_{msy}$, F_{msy}, $1.5*F_{msy}$, and $2.5*F_{msy}$) and simulated changes in biomass and harvest through time.

For the second scenario (i.e. constant harvest), the harvest-biomass line intersects the equilibrium surplus production-biomass curve at two points (A and B in Figure 2b). However, the equilibrium with the smaller biomass is not stable. If biomass drops below the smaller value (A in Figure 2b), then a constant harvest will drive the population to extinction. The second (larger) equilibrium value (B in Figure 2b) is the only stable equilibrium. To sustain a population under a constant harvest, the current biomass must be larger than the smaller biomass (A in Figure 2b) producing that harvest. For a given harvest level (H), we used the model parameters to estimate the two equilibrium biomass values. For Graham-Schaefer models, we simply solved the equation:

$$4*(MSY*B/K)*(1 - B/K) - H = 0.$$

For Pella-Tomlinson models, we used numerical iteration to solve:

$$\gamma*MSY*(B/K)*[1 - (B/K)^{n-1}] - H = 0,$$

which, given n = 1.064, can be expressed as

$$43.825*MSY*(B/K)*[1 - (B/K)^{0.064}] - H = 0.$$

The smaller estimate of equilibrium biomass was compared with current (i.e. year = 2012) biomass to draw conclusions about sustainability of a constant harvest level. The time series of population biomass was derived by solving the ordinary differential equation for each model (equations 1 and 2) with the initial population biomass defined as the estimated current year biomass using the Runge-Kutta (4,5) method described in Dormand and Prince (1980).

Results

The AICc values for each model configuration are presented in Table 2. Overall, the models with constant recreational catchability (T1 – T4) performed better than the density-dependent catchability models (T5 – T12). The models with higher relative weighting of recreational HPUE (e.g. T1 and T3) provided better fits than those with a weighting equal to that for FWIN CPUE (e.g. T4 and T5). The Pella-Tomlinson model (e.g. T3 and T4) fitted the observations marginally better than the Graham-Schaefer model (e.g. T1 and T2). Given these results, we focused only on two model configurations (T1 and T3) when evaluating model implications. Both models assume constant catchability, but they differ in terms of the shape parameter.

The trends in observed recreational HPUE and FWIN CPUE were both in agreement with the surplus production estimates of model T1 and T3 (Figure 3a, b). However, the Graham-Schaefer model (T1) produced higher estimates of biomass (and lower estimates of fishing mortality) than the PT (T3) model (Figure 4a, b).

Estimates of model parameters (K, MSY, B_{1976}, q1 and q2) and management reference points (B_{msy}, B_{2012} F_{msy}, and F_{ext}) are presented in Table 3. The estimates of carrying capacity and F_{ext} were both higher for T3 than those for T1 with relatively high uncertainties. The MSY was estimated precisely by both models with a coefficient of variation (CV) of approximately 5%. Both models provided similar estimates of MSY, F_{msy}, B_{msy}, and the two catchability parameters. The current population biomass is estimated to be ≈18% of B_{msy} for T1 and ≈20% for T3. For the T1 model, the estimated fishing mortality in 2011 (F_{2011}) was 0.64 /yr, which is twice as high as the rate which maximizes harvest (F_{msy} = 0.32). For the T3 model, this degree of over-exploitation was even higher (F_{2011} = 0.79) at 2.25 times F_{msy}. The results indicate that Lake Nipissing walleye population is over-exploited.

The results from simulations which assumed different fishing rates in the future are summarized in Table 4 and Figure 5. The simulations based on T1 predict population biomass could increase to B_{msy} in 4-5 years if there was no fishing; T3 predicts this level of rebuilding would take 9-10 years. Approximately, twice as much time would be needed to rebuild the population to 98% of its carrying capacity. If the population is exploited at F_{msy}, both models predict it will take almost 50 year years (46 for T1, 49 for T3) to reach B_{msy}. If the harvest rate was maintained at 2.5 times F_{msy}, which is higher than the current level, the models differ in terms of biomass trends. T1 predicts that the biomass will be reduced to less than 5,000 kg in 14 years (and eventually to extinction) whereas T3 predicts that the biomass will increase to an equilibrium of 46,000 kg and sustain an annual harvest of 41,000 kg, almost 90% of equilibrium biomass, which may not realistic.

For the constant harvest strategy (starting from the 2012 biomass estimate), the maximum sustainable constant harvest levels (H_{max}) are 24,939 and 39,369 kg for T1 and T3, respectively. Maintaining harvest higher than these values will cause the population to crash. We simulated population biomass dynamics and the relationships among surplus production, current biomass, and harvest levels under two arbitrarily selected constant harvest scenarios, smaller (20,000 kg) and larger (50,000 kg) than H_{max}. Those results are presented in Figures 6 and 7.

Discussion

The surplus production model with constant catchability for the recreational fishery seemed to describe the dynamics of the Lake Nipissing walleye population. The CVs showed that the MSY can be precisely defined, suggesting that the observed population index (the recreational HPUE) may be close to the scenario of up and down isocline of Hilborn and Walters (1992). The other parameters were estimated with relatively high CVs. To improve the accuracy of all parameter estimates, a broader range of population biomass and fishing effort levels from the recreational HUE data is required. The convergence issues associated with a high weighting assignment on FWIN CPUE could be caused by either the short time series (starting in 1998) or weak contrast information of the observations or both. It is expected that the convergence will improve when more information is added in the future.

Although the Pella-Tomlinson model using the shape parameter estimated for marine Perciformes provided a marginally better fit to the observations than the symmetrical Graham-Schaefer model, strong caution should be

exercised when attempting to manage the Lake Nipissing walleye population using this model. First, the choice of the shape parameter value was made from a metadata analysis on marine species and a value has not been estimated for the Lake Nipissing walleye population (a freshwater Percid) due to the lack of suitable information. This study demonstrates that the shape parameter determines the key characteristics of fish population dynamics, including surplus production, MSY and F_{msy} along with the population intrinsic growth rate and its corresponding F_{ext}. Second, the Pella-Tomlinson model with n=1.064 showed strong compensatory population growth and thus presented a long tail toward higher fishing mortality, sustaining high harvests at unrealistically high fishing mortality rates (Figure 10). For example, the Pella-Tomlinson model (T3) showed that the population could sustain a harvest that removed almost 80% (i.e. $2.5*F_{msy}$) of the total population biomass or even higher, contradicting the observations on the Lake Nipissing walleye population. This suggests that the model is not a reliable predictor of the dynamics of this population when fishing mortality is high.

This study provides evidence that the Lake Nipissing walleye population has reached the lowest biomass since 1976 while continuing to be heavily exploited. The current situation places the Lake Nipissing walleye population at high risk. Immediate measures are required to reduce exploitation and allow population biomass to recover. Based on Model T1, the current fishing mortality rate (F=0.64) is very high and approximately equal to the estimated level driving the population to extinction (F_{ext} = 0.64). In particular, when the population is at a low biomass level, any fishing rate higher than F_{msy}, even for a short period of time, will increase the difficulty of restoration and prolong recovery time. To allow the population to recover, three management strategies were modeled:

(1) Declare a moratorium (no harvest) for 7 years to restore the population biomass to the level producing MSY and then use F_{msy} as the harvest policy (see Figure 5, F = 0 for recovery period);
(2) Continue to harvest at the constant harvest rate of F_{msy} (F=0.33, the average of T1 and T3, see F = F_{msy} in Figure 5);
(3) Continue to harvest using a constant harvest less than 36,626 kg per year (the average of T1 and T3, see example in Figure 6).

The first strategy implies fishers must sacrifice short-term benefits for long term gains. However, this could be devastating for anyone who relies on the fisheries for their daily livelihood unless other options, such as the development of other fisheries, are available to compensate for economic losses. Comparing scenarios 2 and 3, option 2 (fishing at F_{msy}) seems more efficient. For the first four years after applying F_{msy}, the harvest would be less than the constant harvest value of 36,626 kg, but starting in year 5, the harvest increases and produces about twice the annual yield in the long run. One drawback of a constant harvest rate (option 2) is that annual harvest will vary with the population biomass and could potentially result in fluctuations in annual walleye supply. The fluctuation of harvest may make it difficult to make investment plans. In contrast, the predictability of future fisheries is relatively high for the constant harvest strategy. The proposed harvest strategies are based solely on the results from a walleye surplus production model and do not allow for interactions with other species in the lake or for variations in lake's ecosystem.

Analyses presented in this paper are based on traditional single-species models of density-dependent changes in per capita growth rate: a compensatory growth assumption (i.e. Schaefer, 1957; Pella and Tomlinson, 1969). Management scenarios based on these models are expected to perform reasonably well when populations are in a "high-abundance domain", but the walleye population in Nipissing can no longer be classified in this domain. Our modeling indicates biomass is less than 20% of the biomass that existed 40 years ago. The population is clearly in a "low-abundance domain", raising concern that cultivation/depensation effects (Walters and Kitchell, 2001) may prevent the population from recovering as predicted by our model predictions. The cultivation/depensation hypothesis assumes that ecosystem dominance by large predatory fish, such as walleye, is due partly to cultivation effects controlling the abundance of forage species that could potentially compete with, or consume, the young of the large dominant predator. Consequently, when the abundance of adult walleye is severely reduced by fishing, the increased abundance of forage species may result in increased predation mortality of walleye eggs and larvae, and reduced survival of juvenile walleye due to predation and/or competition. Depensatory growth was first observed by Allee (1931) and thus called the Allee effect. In addition to the predation and competition effects described above, other factors present in animal populations at a low abundance, such

as mate limitation, cooperative defence and foraging, and habitat alternations, can also cause depensatory growth. A recent monograph (Courchamp et al, 2008) summarizes the many examples of these sorts of effects that have been observed in nature. The Allee effect cannot be detected by simply examining fish recruitment, and instead, the changes in the ratio of fish recruitment versus spawning stock biomass (SSB) at low levels of the SSB can be used to indentify the Allee effect. For Lake Nipissing walleye population, we suggest closely monitoring the ratio of walleye recruitment vs spawning stock biomass since the population has reached its low levels of abundance. Potential depensatory effects are not accounted for in the modeling approach applied in this manuscript. If they exist, then predictions made here are overly optimistic and more stringent management measures may be needed to restore the walleye population to levels that can support a viable fishery.

In addition, the simulation study did not account for estimation uncertainties. Therefore, managers need to take these uncertainties into account when reviewing management options, especially if constant harvest rate and constant harvest policies are under consideration. If such harvest regimes are selected, the population will need to be monitored on an annual or semi-annual basis to determine whether the population is recovering as predicted. If necessary, the management approach may need to be updated within a period of time (e.g. less than 5 years) based on the monitoring results.

We have discussed some of the advantages and disadvantages of surplus production models. The simplified population dynamics is worth emphasizing again. Given the fact that three main population processes, i.e. recruitment, growth, and natural mortality, are aggregated into a surplus process, it is impossible to identify which process(es) is (are) driving the population fluctuations. It is common for fish populations to exhibit high variability in annual recruitment. However, the information used for surplus production modelling is not sufficient to single out recruitment variation. A more sophisticated model, the statistical catch-at-age analysis (SCAA), emerged to model fish population dynamics in the early 1980s after decades of exploration of age-structured models (Fournier and Archibald, 1982; Deriso et al, 1985). This type of modeling requires some important data to be collected from all fisheries, including total harvest, fishing effort and catch-at-age information.

The SCAA traces each cohort observed in fisheries and applies statistical theories as well as fish survival and fishery harvest principles to simulate fish population dynamics and estimate key population parameters, including cohort abundance, fishery recruitment, age (size) specific selectivity, fishing gear catchability, fishing mortality, and their associated variances. If some auxiliary information, such as age-at-maturity and length- (weight) –at-age is available, the SCAA can estimate the time series of the spawning population and recruitment (to the spawning population). Incorporating these parameters estimated from the SCAA, a simulation model can be built to identify growth/recruitment overfishing, assess the historical and current fishing rates, and evaluate different harvest policies including different size limits, harvest rules, and quota allocations.

To summarize, the SCAA and the corresponding simulation model can assist with decision-making under uncertainty, e.g. see the management strategy evaluation procedure proposed by Smith et al (1999). We suggest that the information required for an age-structured model be added to the current monitoring program on Lake Nipissing and that the SCAA be a future tool developed to inform the management of the Lake Nipissing walleye population.

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Table 1. Model configurations

Treatment	Model	Catchability	Data Weight
T1	Graham-Schaefer	$q_1 = c$	5:5:1
T2	Graham-Schaefer	$q_1 = c$	5:5:5
T3	Pella-Tomlinson	$q_1 = c$	5:5:1
T4	Pella-Tomlinson	$q_1 = c$	5:5:5
T5	Graham-Schaefer	$q_1 = c*B^{-0.5}$	5:5:1
T6	Graham-Schaefer	$q_1 = c*B^{-0.5}$	5:5:5
T7	Pella-Tomlinson	$q_1 = c*B^{-0.5}$	5:5:1
T8	Pella-Tomlinson	$q_1 = c*B^{-0.5}$	5:5:5
T9	Graham-Schaefer	$q_1 = c*B^{-0.35}$	5:5:1
T10	Graham-Schaefer	$q_1 = c*B^{-0.35}$	5:5:5
T11	Pella-Tomlinson	$q_1 = c*B^{-0.35}$	5:5:1
T12	Pella-Tomlinson	$q_1 = c*B^{-0.35}$	5:5:5

Table 2. The calculated AICc for models grouped by two weight scenarios.

Model	AICc	Weight	Evidence Ratio
Weight: 5:5:1			
T3	109.6	0.77	1
T1	112.08	0.22	3.44
T11	119.69	0.005	154.84
T9	121.99	<0.002	>490
T7	126.53	<<0.001	>4700
T5	110.38	<<0.001	>5500
Weight: 5:5:5			
T4	128.44	0.51	1
T2	129.12	0.47	1.08
T12	137.85	0.006	85
T10	138.25	0.005	103
T6	143.12	0.004	1186
T8	143.38	0.004	1328

Table 3. The estimated and derived parameters from the surplus production model for Lake Nipissing walleye

Note: The lake surface area was assumed to be 87,325 hectare.

Model		T1		T3	
Estimated Parameters	Units	Value	CV	Value	CV
Shape (n)		2		1.064	
Carrying capacity (K)	kg (kg/ha)	486560 (5.57)	0.48	588370 (6.74)	0.48
MSY (m)	kg (kg/ha)	76250 (0.87)	0.04	78720 (0.90)	0.05
Catchability – Recreational(q_1)	per hr	$3.79*10^{-7}$	0.39	$4.9*10^{-7}$	0.33
Catchability – FWIN (q_2)	per net	$2.50*10^{-5}$	0.41	$3.33*10^{-5}$	0.37
Biomass in the first year (B_{1976})	kg	312330 (3.58)	0.33	241820 (2.77)	0.27

Derived Parameters	Units	Value	CV	Value	CV
B_{msy}	kg (kg/ha)	243280 (2.79)	0.48	223580 (2.56)	0.48
B_{2012}	kg (kg/ha)	43712 (0.50)	0.5	43855 (0.50)	0.37
F_{ext}	per year	0.64	0.49	5.86	0.46
F_{msy}	per year	0.32	0.49	0.35	0.46

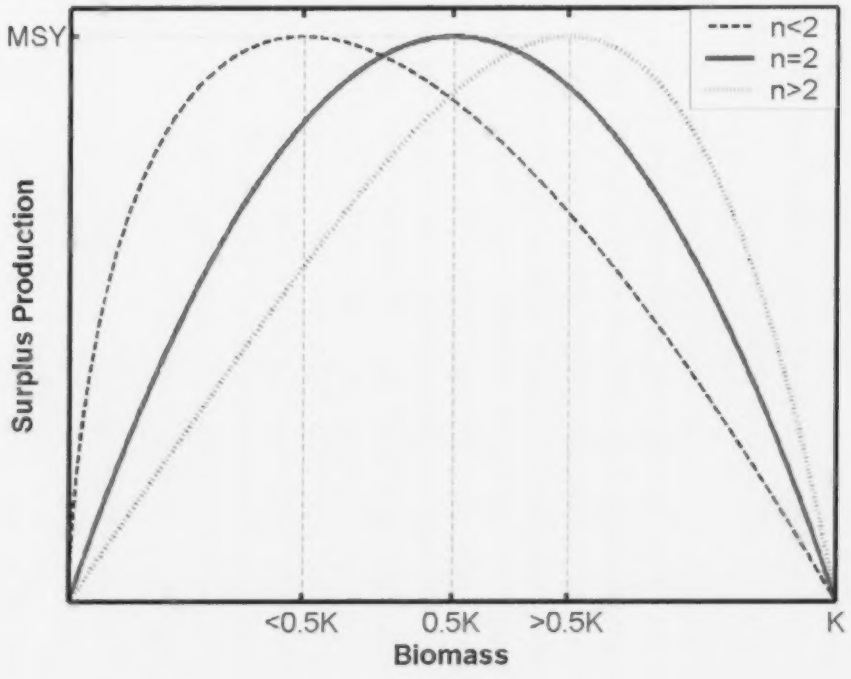
Table 4. Results of simulations using different constant harvest rates (fishing mortality) by Graham-Schaefer (T1) and Pella-Tomlinson (T3) surplus production models (refer to the text for a detailed description).

	Total Fishing Mortality (F)				
T1 (F_{msy}=0.32)	F=0	F=0.5*F_{msy}	F=F_{msy}	F=1.5*F_{msy}	F=2.5*F_{msy}
Equilibrium Biomass	486560	364920	243280	121640	0
(kg or kg/ha)	5.58	4.18	2.79	1.39	0
Equilibrium Harvest	0	57187	76250	57187	0
(kg or kg/ha)	0	0.65	0.9	0.65	0
Years to Equilibrium	29	33	46	79	14 (B<5000)*
T3 (F_{msy}=0.35)	F=0	F=0.5*F_{msy}	F=F_{msy}	F=1.5*F_{msy}	F=2.5*F_{msy}
Equilibrium Biomass	588370	371536	224907	137873	46364
(kg or kg/ha)	6.74	4.25	2.58	1.58	0.53
Equilibrium Harvest	0	33939	78720	71694	40800
(kg or kg/ha)	0	0.39	0.9	0.82	0.46
Years to Equilibrium	41	47	49	49	34

* After 14 years of harvest at F=2.5*F_{msy}, the population biomass was reduced to 5,000 kg and continued to decline until extinct.

Figure 1. The relationships (a) between biomass and surplus production and (b)between equilibrium biomass or harvest and fishing mortality rate under different shape parameter (n) values of the general surplus production model, i.e. Pella-Tomlinson model. (Note: n=2, the model reduced to Graham-Schaefer model).

(a)



(b)

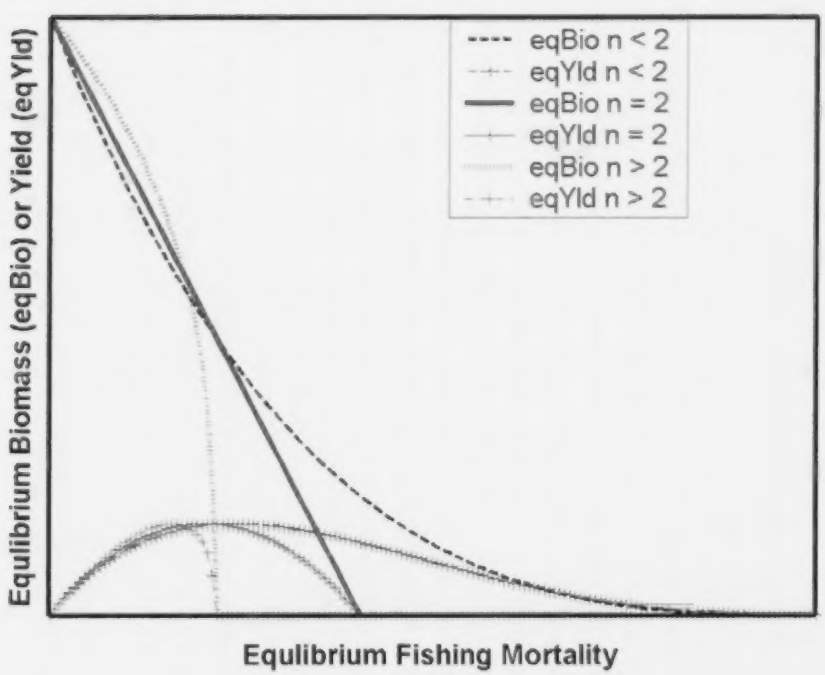
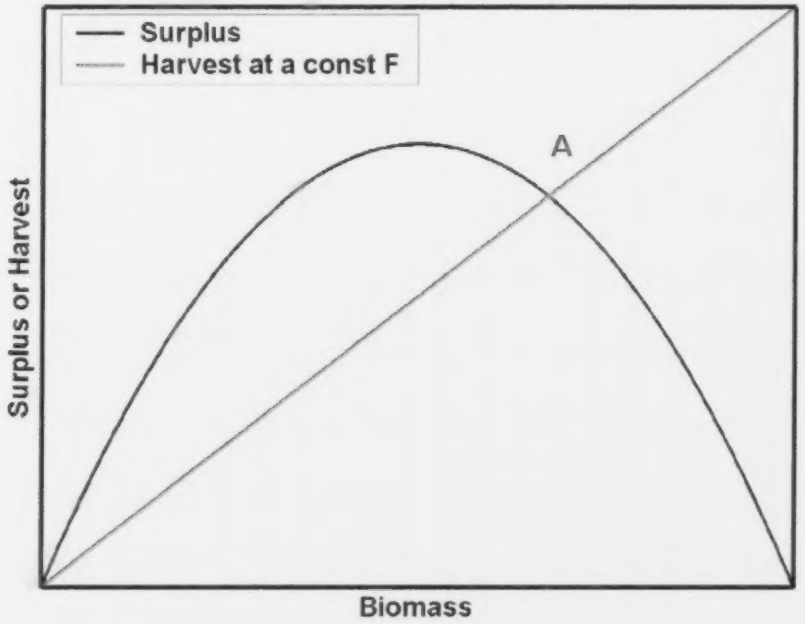


Figure 2. The relationship between population biomass and surplus production under (a) constant harvest rate (fishing mortality rate) and (b) constant harvest: an example of Graham-Schaefer model.

(a) Note: A is a stable equilibrium under a large and a small fishing mortality rate, respectively.



(b) Note: A (small) and B (large) are two equilibria under a constant harvest level; A is unstable and B is stable.

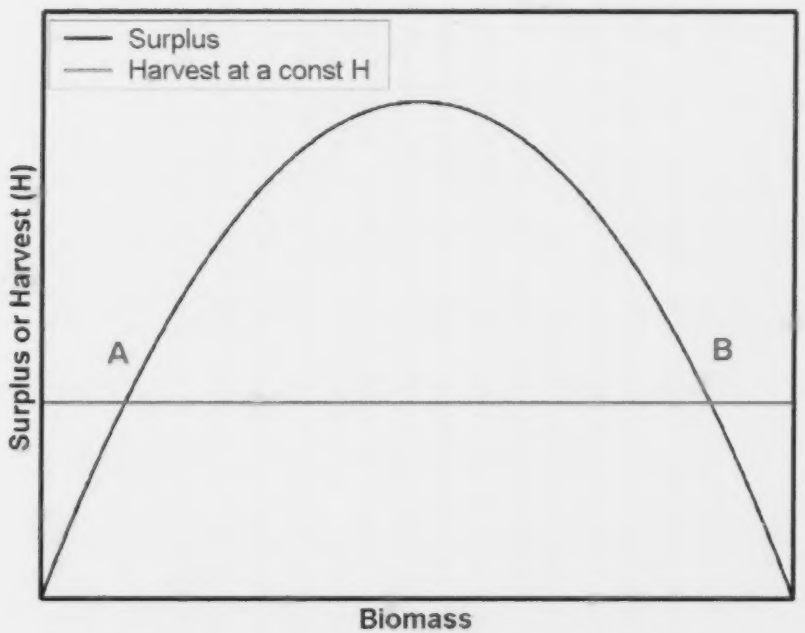
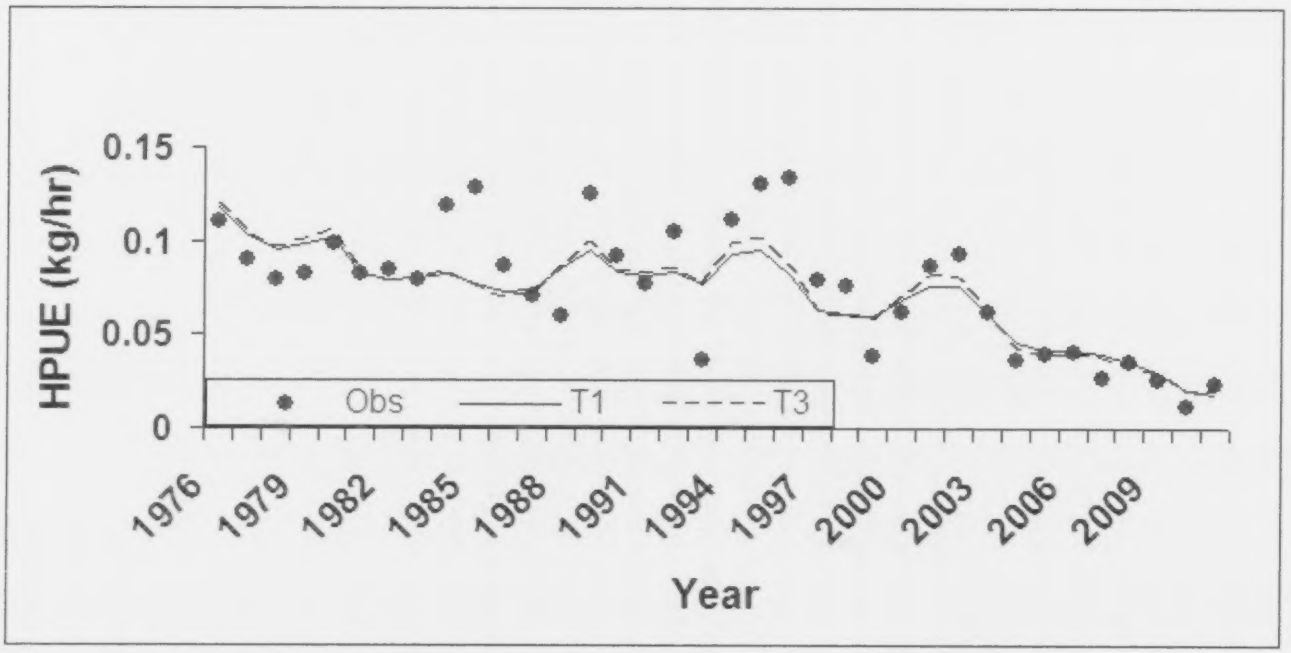


Figure 3. Plots of predicted and observed (a) recreational HPUE (kg•hr^{-1}) and (b) FWIN CPUE (kg•net^{-1}) for Graham-Schaefer model (T1) and Pella-Tomlinson model (T3).

(a)



(b)

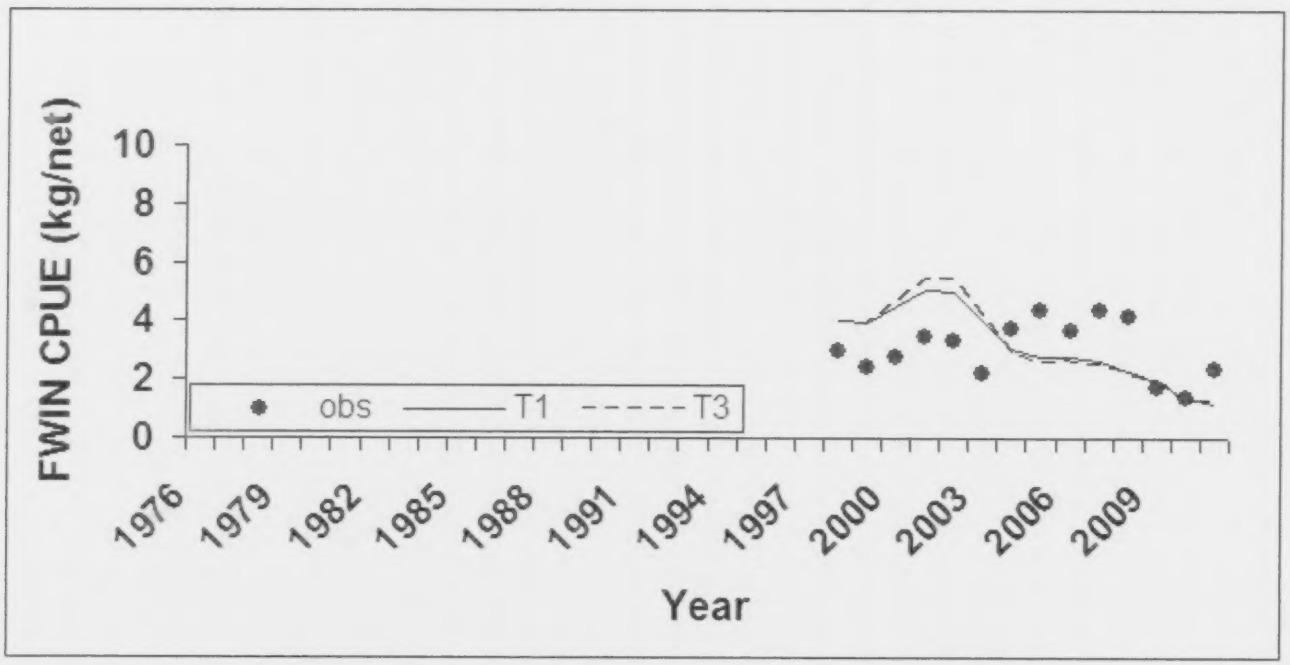
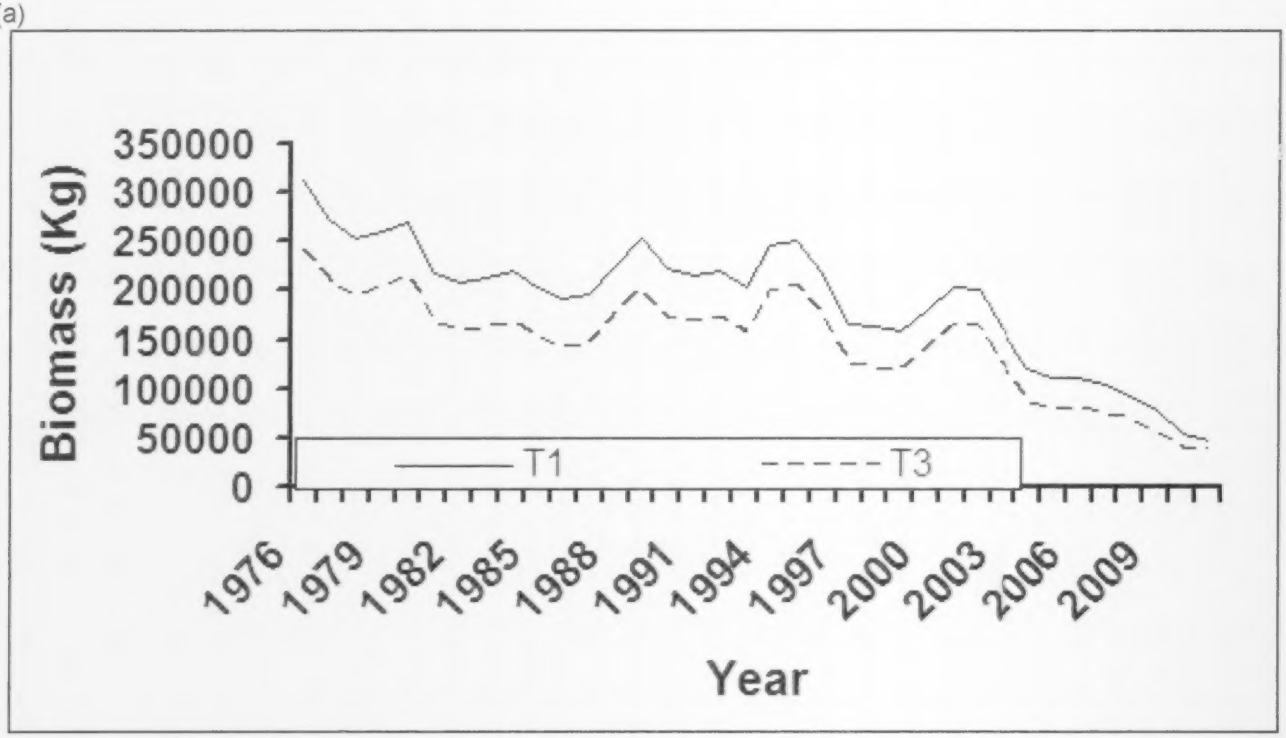


Figure 4. Time series of (a) estimated biomass (kg) and (b) total fishing mortality rate (F) for Graham-Schaefer model (T1) and Pella-Tomlinson model (T3).

(a)



(b)

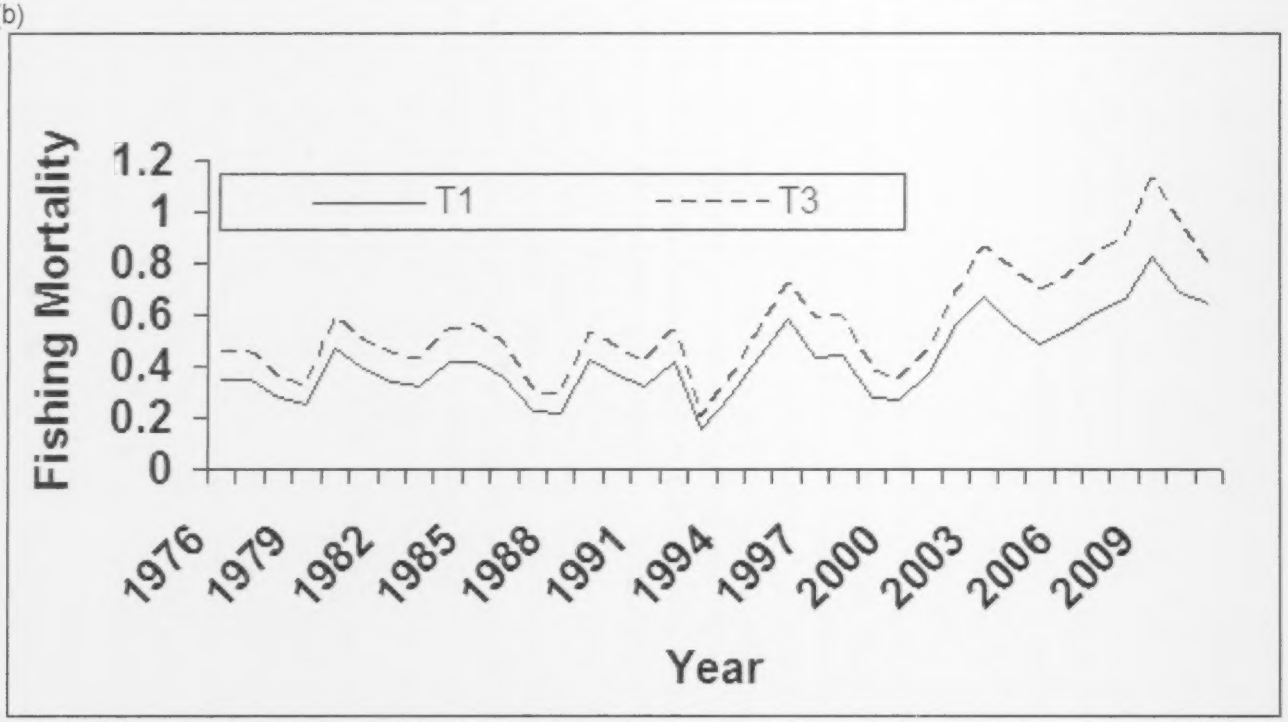


Figure 5. Trajectories of 50-year simulated population biomass (kg) (the top panels) and the predicted harvest (kg) (the bottom panel) under different constant harvest rates for Graham-Schaefer model (T1—the left panels) and Pella-Tomlinson model (T3—the right panels) for Lake Nipissing walleye (note: refer to the text for a detailed description).

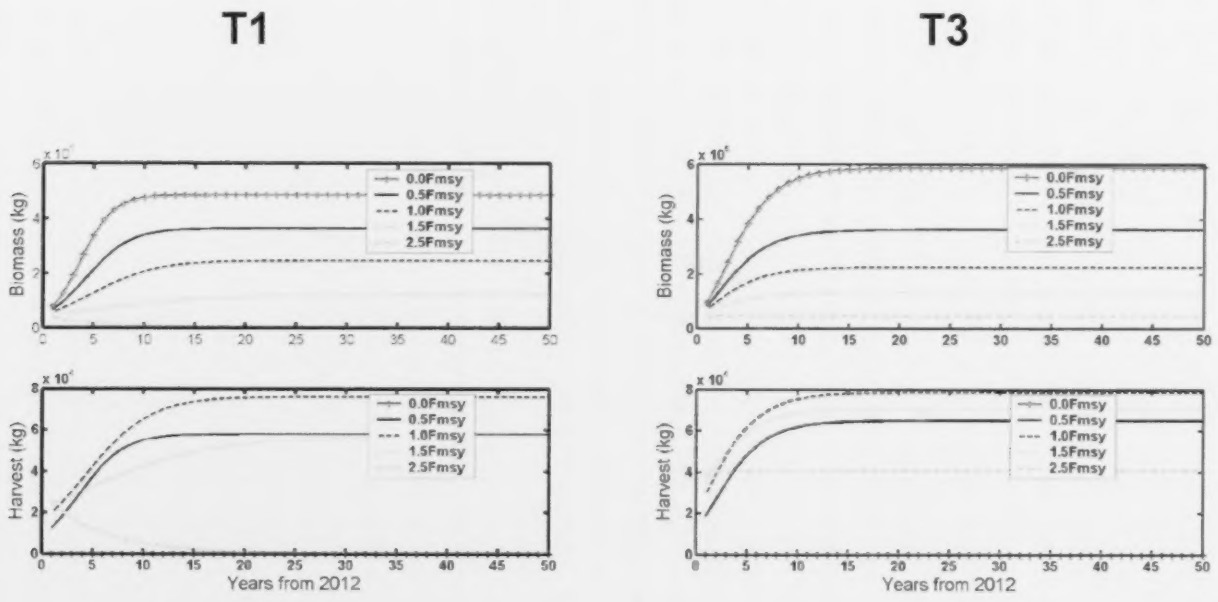


Figure 6. Trajectories of simulated population biomass (kg) (the top panels) and the locations of two equlibria (intersections between the biomass-surplus production curve and a constant harvest line) relative to the sustainable harvest level estimated by 2012 biomass (the bottom panel) under a constant harvest of 20000 kg for Graham-Schaefer model (T1—the left panels) and Pella-Tomlinson model (T3—the right panels) for Lake Nipissing walleye (note: refer to the text for a detailed description).

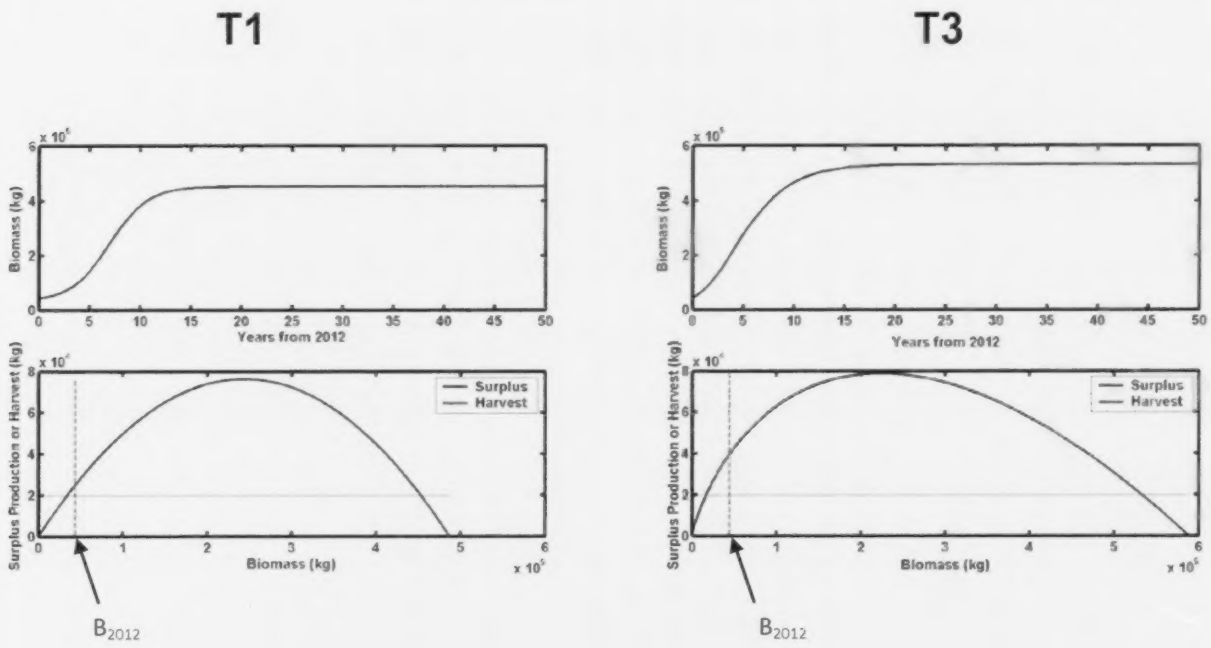


Figure 7. Trajectories of simulated population biomass (kg) (the top panels) and the locations of two equlibria (intersections between the biomass-surplus production curve and a constant harvest line) relative to the sustainable harvest level estimated by 2012 biomass (the bottom panel) under a constant harvest of 50000 kg for Graham-Schaefer model (T1—the left panels) and Pella-Tomlinson model (T3—the right panels) for Lake Nipissing walleye (note: refer to the text for a detailed description).

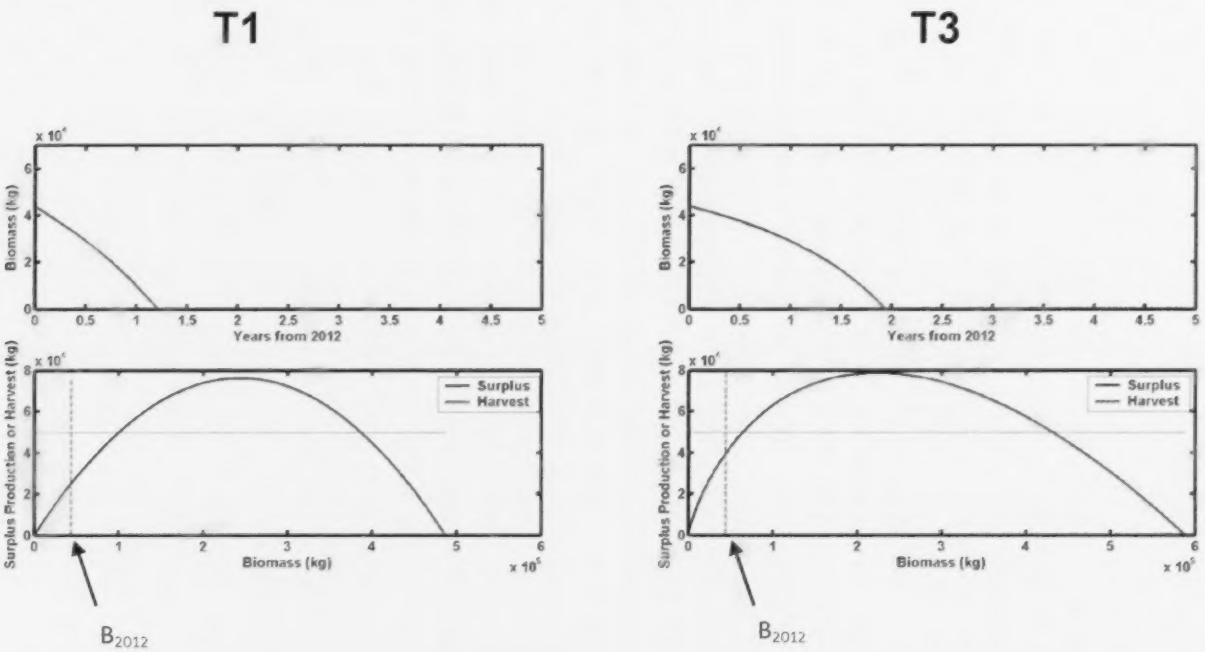
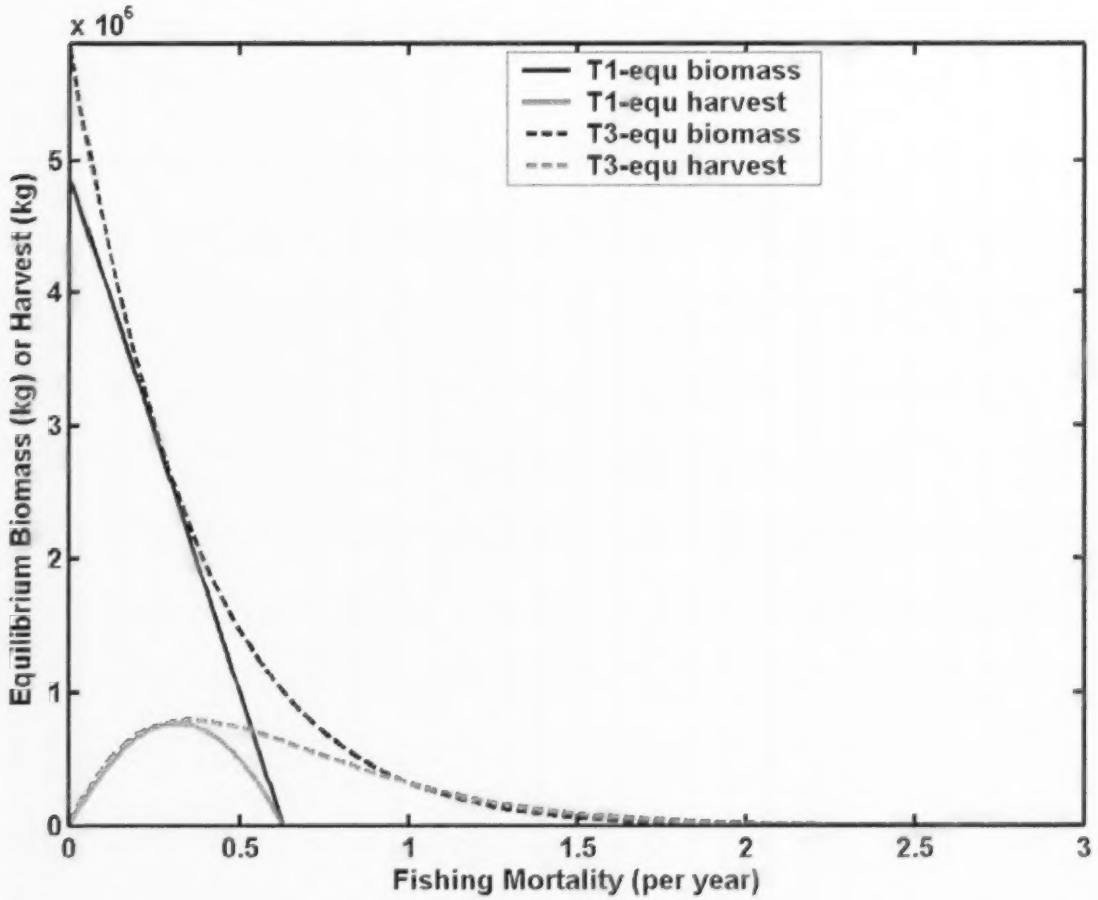


Figure 8. The relationship between equilibrium biomass (kg) and harvest (kg), and fishing mortality (F) for Graham-Shaefer model (T1) and Pella-Tomlinson model (T3) for Lake Nipissing walleye.



Appendix. Data used for fitting a surplus production model for Lake Nipissing walleye population.

Year	Total Harvest (kg)	Recreational Harvest Per Effort (kg/hr)	FWIN Catch Per Effort (kg/net)
1976	109718	0.11	
1977	94908	0.09	
1978	69347	0.08	
1979	65987	0.08	
1980	126789	0.10	
1981	84490	0.08	
1982	71442	0.08	
1983	68342	0.08	
1984	91343	0.12	
1985	85059	0.13	
1986	69326	0.09	
1987	43708	0.07	
1988	49431	0.06	
1989	107060	0.13	
1990	81555	0.09	
1991	69684	0.08	
1992	92577	0.10	
1993	31703	0.04	
1994	71615	0.11	
1995	109061	0.13	
1996	126913	0.13	
1997	73078	0.08	
1998	72092	0.08	3.00
1999	44505	0.04	2.43
2000	49134	0.06	2.80
2001	75845	0.09	3.46
2002	112717	0.09	3.35
2003	108038	0.06	2.20
2004	68074	0.04	3.72
2005	53797	0.04	4.36
2006	59130	0.04	3.65
2007	63231	0.03	4.39
2008	61084	0.03	4.16
2009	65075	0.03	1.77
2010	37646	0.01	1.40
2011	30366	0.02	2.36

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